# Hyperacute motion detection by the lateral eyes of jumping spiders

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Abstract

Jumping spiders (Salticidae) are renowned for their high performing visual system. In addition to their prominent forward-facing telescope-like principal eyes, salticids possess two or three pairs of secondary eyes used for wide-angle motion detection. Salticids orient towards relevant sources of motion detected by the secondary eyes, enabling them to inspect the stimulus with their spatially acute principal eyes. The anteriormost pair of secondary eyes, the anterior lateral (AL) eyes, also faces forward and has higher spatial acuity than the other, laterally-facing, secondary eyes. We used small computer-generated targets to elicit orienting saccades from tethered jumping spiders in order to examine the perceptual limits of the AL eyes. We describe the contrast thresholds of male and female spiders, investigate the reaction time between stimulus appearance and initiation of orientation, as well as the minimum distance a stimulus must travel before eliciting a saccade. Our results show that female spiders react to lower contrast stimuli than males and demonstrate that the secondary eyes can detect stimulus displacements considerably smaller than the inter-receptor angle.

Keywords: Jumping spider, Motion detection, Hyperacuity, Salticidae, contrast threshold

## 1. Introduction

Jumping spiders use outstanding eyesight to locate, stalk and finally pounce on their prey (Jackson & Pollard, 1996). Their principal eyes function like moveable miniature telescopes (Land, 1969a; Williams & McIntyre, 1980) and are specialised for high resolution vision (Land, 1969b), but are limited by their small field of view. The three pairs of secondary eyes have wide fields of view which collectively encompass up to 360° (Homann, 1928) and are especially sensitive to motion (Duelli, 1978; Land, 1971; 1972; Zurek et al., 2010) but also support high spatial acuity, owing to densely spaced, optically isolated photoreceptors (Eakin & Brandenburger, 1971). Targets detected by the secondary eyes lead to turning movements of the spider, with the goal of centering the object of interest in a frontal fixation region in the field of view of the principal eyes for closer inspection. Among the secondary eyes, it is the anterior-lateral (AL) eyes that are especially interesting. Due to having both a wide field of view with considerable binocular overlap, as well as a central acute zone (Homann, 1928; Land, 1985), they are likely involved in other aspects of visual processing (Forster, 1979; Zurek et al., 2010) in addition to motion detection.

For an eye to be able to reliably detect motion and to locate the origin of it, sufficiently high spatial acuity is needed, as well as receptor kinetics fast enough to limit motion blur. Unsurprisingly, fast flying insects, having to cope with extreme angular speeds, possess some of the fastest photoreceptors known (Gonzalez-Bellido, Wardill,

& Juusola, 2011). The contrast threshold for behavioral responses to moving targets is dependent on both spatial and temporal resolution, as well as on the amount of reduction in light flux in one photoreceptor that is sufficient for eliciting response (Nordström, Barnett, & O'Carroll, 2006; Vallet & Coles, 1991). While the detection of fast targets is a challenge for a visual system, the same holds true for very slow movement. Theoretically, stimuli can be detected when at least two receptors are sufficiently stimulated in succession (Hassenstein & Reichardt, 1956). Generally this equates to a minimum detectable stimulus movement of at least one inter-receptor angle, however, higher order integration can enable the detection of even smaller displacements ('hyperacuity'; Westheimer, 1975). Field observations of the eucalypt bark-dwelling salticid *Servaea vestita* (Koch) orienting to the most miniscule of motions compelled us to investigate the limits of this ability. In particular, we determined the minimum reaction time to orient to a stimulus, the stimulus contrast threshold leading to orienting behavior, and the minimum angular distance a stimulus has to travel before it can be detected.

## 2. Methods

### *2.1 Experimental setup*

Because these methods are almost identical to those described in Zurek et al. (2010), only an overview and relevant details will be provided here. Firstly, all eyes except for the anterior lateral (AL) eyes were covered with dental silicone (Coltene Whaledent) by restraining spiders without the need for anaesthesia, following methods described in Zurek et al. (2010). The dental silicone is opaque and removable, and no detrimental short- or long-term effects were observed. Spiders were suspended from and adjustable frame by thin wire attached to the cephalothorax by a drop of wax. For stimulus presentation, we used two 17" TFT screens (resolution 1280x1024 px, 75Hz) placed at an angle of 120° with respect to one another on a vibration isolation table (Kinetic Systems). Color, contrast, and brightness levels of the screens were equalised and calibrated using an Eye One colorimeter (X-Rite Inc). Spiders were filmed at 60 fps.

Stimuli were generated using Vpixx v2.36. As we used small dark targets on uniform grey background, we defined contrast as $I_{stimulus} - I_{background}/I_{background}$ (Peli, 1990). Spiders were placed 150 mm away from the screen, and at this distance 1 pixel equated to 0.1°. At speeds slower than 1 °/s, spiders were positioned further away from the screen (300 mm at 0.5°/s, and 600 mm at 0.25°/s) and stimulus size was increased accordingly. Suspended spiders held on to a polystyrene ball (diameter 15 mm) marked with crosshair lines, which spiders could easily turn and grasp without dropping for several hours (Zurek et al., 2010). Stimuli elicit a series of whole-body saccades with

magnitude corresponding to stimulus position (Zurek and Nelson, 2012), which lead to a turn of the ball in the opposite direction. It has previously been shown that the moment of inertia of the ball is low enough that it can be assumed not to impact orientation turns (Land, 1972; Zurek and Nelson, 2012).

*2.2 Contrast threshold tests*

Spiders were starved for 5-7 days prior to testing in order to maximise responsiveness to visual stimuli (Zurek et al., 2010). In order to test contrast thresholds for orienting responses mediated by the AL eyes, we used an interleaved staircase protocol for the presentation of stimuli. Each spider (female N=10, male N=9) was given 50 trials with a 3° square stimulus, which were randomly presented on either the left or right screen, (same number of stimuli for both sides). Stimuli appeared outside the AL eye field of view at the peripheral edge of the screens, 10° below horizon and moved at 10°/s towards the screen center. To avoid habituation, a pause of 2 min was inserted after every stimulus presentation. This size and speed is comparable to biologically relevant stimuli evoking responses, and has previously elicited maximum response rates from *S. vestita* (Zurek et al., 2010).

Two alternating lists of contrast values were used to determine which stimulus was used: one of the lists started with contrasts rising from 0.01 to 1 and one descending from 1 to 0.01. Below a contrast of 0.1 the steps differed by 0.005 units; above 0.1 the step size was increased (see Fig.1). Within each staircase, when the spider responded to a contrast, the following lower contrast was used. If no response

occurred, the following higher contrast stimulus was used. This method leads to an equilibrium contrast at which both staircases oscillate around the perceptual threshold, with most of the 50 samples crowded around it. The averages of the responses were computed separately for both sexes, and were fit with Weibull cumulative distribution functions,

$$f(x;k,\lambda) = 1 - e^{-(x/\lambda)^k}, \quad (1)$$

with x being the response rate, $\lambda$ the scale parameter (inflection point) and *k* the shape parameter (slope) of the curve. $\lambda$ and *k* are free parameters. In order to force the fit to near zero values at very low contrasts, the data were 'padded' with zero-response values at contrasts that were below the minimum detected contrast of each sex. Best-fit values for females and males were compared using an Extra sum-of-squares F test as implemented in Prism v5.0.

Appearance of stationary stimuli rarely elicits saccades from salticids (Duelli, 1978; Land, 1971). We verified that this holds true in our setup by running controls with stationary maximum contrast stimuli (N=10, n=40). These trials elicited only two responses.

*2.3 Reaction time tests*

We used two different stimulus sizes to test for reaction time, here defined as the time between stimulus appearance and initiation of the first saccade (determined by first video frame in which the stimulus was visible, and first frame showing displacement of the ball) and, by extension, the minimum distance that a stimulus needs to cover in order to elicit a saccade.

a) We tested for sex differences using maximum contrast square stimuli with an edge length of 3°, moving at 1, 9, or 27°/s. Both female (N=13) and male (N=11) spiders were suspended as described above, with stimuli appearing on either the left or right screen inside the field of view of the AL eyes (at 35.5° laterally, n=2 stimuli per speed and spider). For *S. vestita,* the average inter-receptor angle in the corresponding retinal area has been ophthalmologically determined to be 1° (David C. O'Carroll, pers. comm.). For comparison, the salticid with the highest spatial acuity described so far, *Portia fimbriata*, achieves 0.55° in the acute zone and 0.97° at the lateral margins of the retina (Land, 1985). Two stimuli at each velocity were presented to each spider, one per side, in randomised order. In trials where the spider responded, reaction time was determined, and angle travelled by the stimulus was calculated. As the screens are flat, the angular velocity varies slightly during the path of the stimulus, and the calculated stimulus positions were adjusted to take this into account. Two-way ANOVAs were used to test for effects of stimulus speed and sex on reaction time and stimulus travel.

b) In order to investigate the perceptual limits of the system, a smaller stimulus subtending less than one inter-receptor angle was used (0.5° edge length). The stimulus appeared at 35.5° laterally and was presented to 10 females at velocities of

0.25, 0.5, 1 and 9°/s (n=20 each for 0.25, 0.5, 9 °/s and n=60 for 1°/s). Data from trials where spiders responded were analysed as described under 1.

## 3. Results

### *3.1 Contrast threshold*

First, we investigated target contrast thresholds in female and male spiders (Fig.1). We found a superlinear increase in response at low contrasts, and significant sex differences in the psychometric functions (Extra sum-of-squares F test for scale parameter $\lambda$ and shape parameter *k*, F=2308, df=2, p<0.0001). Female spiders had a lower contrast threshold for orienting responses than males (female: =0.083, C50=0.076; male: =0.223, C50=0.192), as well as a steeper slope of the psychometric function (Fig. 1).

### *3.2 Reaction time*

Next, we investigated reaction time to high contrast stimuli appearing within the field of view, and determined the minimum distance a stimulus must travel before being detected by the AL eyes. Two different angular stimulus sizes were used:

a) We presented 3° square stimuli to both sexes, and found that sex had no effect on reaction time *T* (2-way ANOVA, F=0.002, df=1, p=0.969) (Fig. 2a). *T* significantly decreased in response to higher stimulus velocities (F=6.828, df=2, p=0.002). Consequently, travel distances before a response increased with stimulus velocity (F=123.3, df=2, p<0.001) equally for both sexes (F=0.323, df=1, p=0.571) (Fig. 2b). Overall, the minimum reaction time at all stimulus velocities was between 80 and

120 ms, corresponding to minimum stimulus travel distances of approximately 0.1° (equivalent to 1 pixel on screen) at 1°/s, 1° at 9°/s, and 2.5° at 27°/s. As minimum stimulus travel was only a tenth of the inter-receptor angle at slow speed, we decided to investigate even smaller displacements using stimuli that subtend angles below the acceptance angle of the receptors.

b) Next, we presented 0.5° square stimuli to females, and determined minimum detected stimulus travel for four different stimulus velocities (Fig. 3a). Moving at 1°/s, even these small stimuli were consistently detected at travel distances below 1° (Fig. 3b). At very slow speeds of under 1°/s, stimuli were often responded to only after long delays, which lead to comparatively long stimulus travel distances. The high variation in detected stimulus travel at the slower speeds indicates that they lie at the limit of what the spiders could perceive as motion.

**4. Discussion**

We found that *S. vestita* were able to detect angular movement considerably smaller than the inter-receptor angle of photoreceptors in their AL retina and that females have a markedly lower contrast threshold for orientation responses than males. Visual reaction times were comparable to other animals across phyla (humans (Brebner & Welford, 1980), monkeys (Saslow, 1972) and female houseflies (Srinivasan & Bernard, 1977), all with average reaction times between 150 and 300 ms), but were slower than those of insects specialised for detection of fast objects, such as male houseflies,

dragonflies and tiger beetles, all of which achieve reaction times below 50 ms (Gilbert, 1997; Srinivasan & Bernard, 1977).

Land (1971) observed orientation turns of salticids in response to stimulus movements of 1°, which is close to the inter-receptor angle the posterior lateral (PL) eyes and this has since been assumed as the minimum detectable movement. We show here that stimulus motion is detected by the AL eyes even when it is smaller than the inter-receptor angle. A comparable observation was recently made in the ctenid spider *Cupiennius salei* (Fenk & Schmid, 2010), where gratings with wavelength smaller than twice the inter-receptor angle of the lateral eyes elicited saccades of the AM retinae. Optical resolution does require this minimum angular separation, but target detection can be achieved with less salient stimuli. Hoverflies possess small target motion detecting neurons that respond to moving targets subtending much smaller angles than the receptive fields of single photoreceptors (Nordström et al., 2006). In humans, it has been found that 'hyperacute' discrimination abilities of a visual system other than spatial acuity can exceed the limits dictated by inter-receptor angles (Westheimer, 1975). For example, while the human eye can only discriminate two parallel lines as separate if they are at least 1 minute of arc (0.0167°) apart, a misalignment of $1/10^{th}$ of that distance can be detected without problems, a phenomenon known as Vernier acuity. Motion hyperacuity, which can be an order of magnitude more sensitive than spatial acuity, is a similar phenomenon. Motion hyperacuity has not yet been described in spiders, but is well understood in humans (Westheimer, 2009) and a number of other vertebrates, such as rabbits (Collewijn, 1972; Grzywacz, Amthor, & Merwine, 2009) and owls (Harmening, Gobbels, & Wagner, 2007). In insects, the phenomenon has been

described in dipterans, where grating displacements of a tenth of the interommatidial angle were sufficient to elicit responses from large-field motion detecting H1 neurons (Coombe, Srinivasan, & Guy, 1989; Moya, Wilcox, & Donohoe, 1992). Unlike the small targets we used, these gratings covered a large part of the visual field of the eye, and input from many ommatidia could be integrated.

Hardie and Duelli (1978) found that the width of the angular sensitivity function of a PL eye photoreceptor at the 50% response level was 0.89° ± 0.12° in *S. vestita*. As the AL eyes share many characteristics with the PL eyes (Blest, 1983; Eakin & Brandenburger, 1971), and the inter-receptor angle of ~1° in the relevant area in our study is close to conditions in the PL retina (Duelli, 1978), the sensitivity function of the photoreceptors is likely similar. The photoreceptors of salticid secondary eyes are optically isolated from each other by pigment sheaths (Blest 1983) and therefore optical crosstalk should have no influence on minimum detected stimulus motion. The image of the larger stimulus used here falls on at least 9 receptors simultaneously, and a small stimulus displacement would lead to small light intensity modulations in all receptors at the edge of the image. However, the small stimuli used here subtended an angle that is smaller than one inter-receptor angle, and small displacements were still detected. In this case, hyperacute motion detection by AL receptors with assumed gaussian sensitivity distribution and a full function width of 1° at 50% response may arise because a centered, full contrast 0.5° stimulus would lead to 22.7% reduction in light falling on the receptor it is centered upon, and to only 1.2% reduction in the adjacent receptors, based on the volume integral of the three-dimensional sensitivity function (Fig. 4). When the stimulus moves by 0.2°, the combined change in photon flux

on the three adjacent receptors would be 12.3% (left and central receptors experiencing an increase, and the right receptor experiencing a decrease in photon flux), which is above the contrast threshold we determined. However, the exact acceptance angle of the receptors in question is still unknown, so these values should be viewed with caution.

The changes in receptor potential are likely integrated upstream by a correlation type motion detection unit (Hassenstein & Reichardt, 1956), as indicated by the superlinear increase in response to increasing contrast at low contrast values. Perhaps it is not surprising that jumping spiders, whose behavior is largely dominated by vision, exhibit hyperacute sensitivity to motion. Duelli (1978) hypothesised a movement detecting unit in the salticid *Evarcha arcuata* using similar methods as in our study, but because of the considerable difficulty obtaining electrophysiological recordings from salticid neurons, no higher order neurons responding specifically to visual motion have been described to date.

Not much is known about sex differences in contrast perception in non-human animals. Some dipterans show sexual dimorphism in their visual systems, such as the dorsal 'bright zone' of male hoverflies that allows for increased contrast sensitivity (Straw, Warrant, & O'Carroll, 2006), and the higher spatial acuity of male houseflies compared with females (Franceschini et al., 1981; Hornstein et al., 2000). However, the apparent higher contrast sensitivity we found among female salticids may be underpinned by differences in motivation rather than physiology *per se,* as we found no sex differences in reaction time. Further, the steeper slope of the psychometric function

in females indicates higher consistency in orientation propensity, and male salticids appear to be less likely to complete behavioral tasks (Jackson & Hallas, 1986; Jackson & Pollard, 1996; Zurek et al., 2010), possibly due to lower nutritional demands (Givens, 1978) and a resulting lower motivation to investigate potential prey. In the field, a lower contrast threshold for orientation turns could potentially translate to more detected prey items.

*S. vestita's* visual reaction times seem slow when compared with fast-moving insects, and these differences are likely adaptations to the distinct challenges posed by different natural history. Male houseflies profit from their fast visual reaction time when they chase conspecifics, and tiger beetles, which prefer to attack fast moving prey (Layne, Chen, & Gilbert, 2006), must react quickly during their characteristic stop-and-go chases. Flies and tiger beetles excel at rapid responses to high velocity stimuli while *S. vestita* are slower to react, but are extremely sensitive to small movements. These responses are well suited to their foraging strategy of sit-and-wait followed by stealthy stalking. High-speed chases are rare, and stimuli moving at velocities that flying insects encounter are of little interest to a jumping spider, while the detection of small prey items at a distance is of considerable importance. These results provide another compelling example of how the unique lifestyle and ecology of animals is mirrored by their visual systems (O'Carroll et al., 1996).

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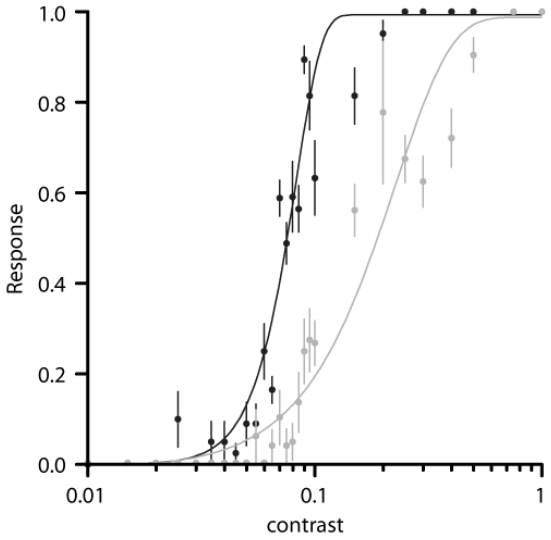


Figure 1. Psychometric functions of female (black, N=10, n=500, $R^2$=0.9636. $\lambda$ = 0.083±0.0004, *k*=3.852±0.099) and male (grey, N=9, n=450, $R^2$=0.9440. $\lambda$ = 0.228±0.0025, *k*=1.79±0.028) spiders responding to moving targets of different contrast. Data points represent mean response ± SEM.

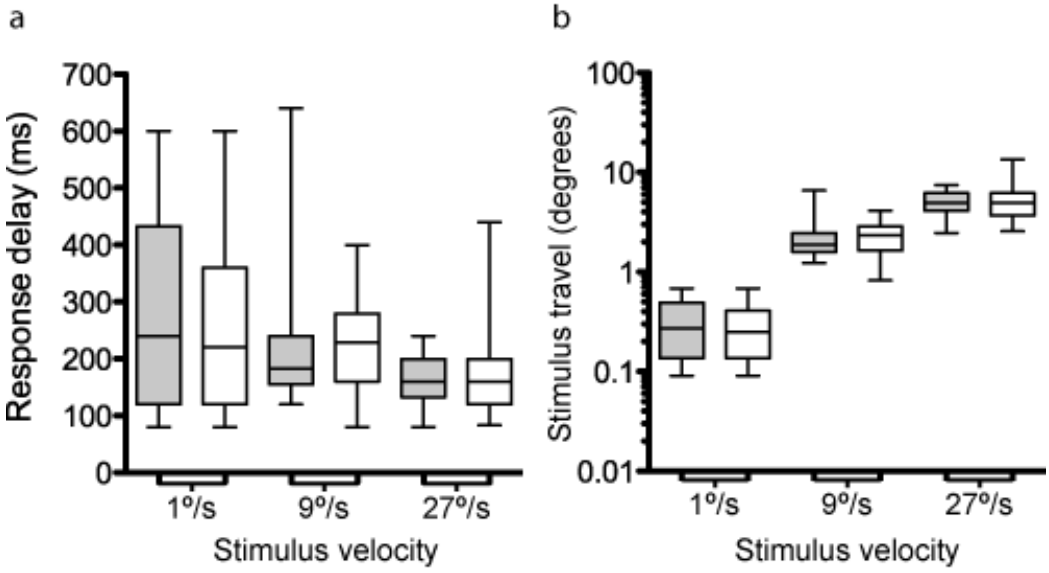


Figure 2. a) Reaction time between appearance of 3° square stimulus and initiation of the first saccade by female (white, N=13) and male (grey, N=11) spiders at velocities of 1°/s (female n=16, male n=15), 9 °/sec (female n= 26, male n= 21) and 27 ° /sec (female n=25, male n=18). Whiskers represent min and max response delay. b) Stimulus travel distance between stimulus appearance and initiation of the first saccade. Whiskers represent min and max travel distance.

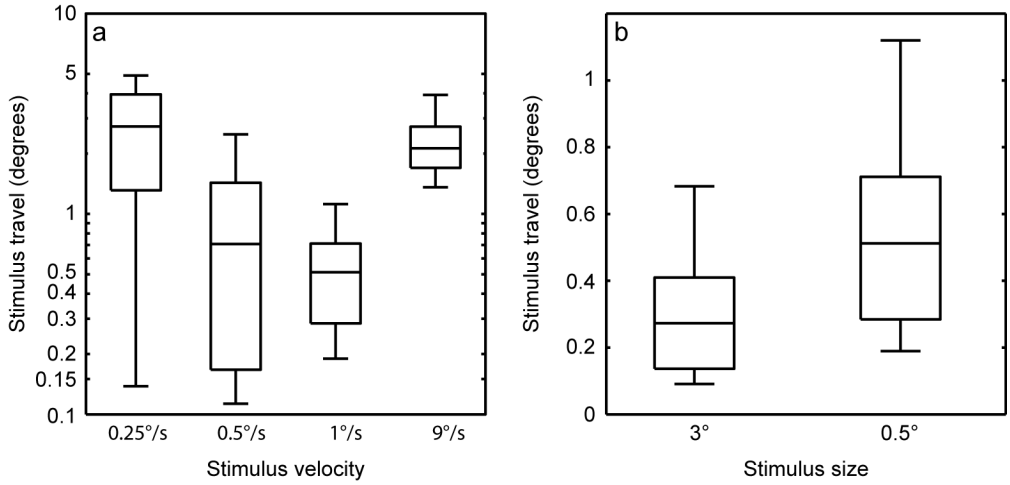


Figure 3. a) Median travel distance between appearance of 0.5° square stimulus and initiation of the first saccade by female spiders (N=10) at velocities of 0.25°/s (n=14), 0.5°/sec (n=16), 1° /sec (n=32), 9°/s (n=16). Whiskers represent min and max travel distance b) Comparison of travel distance for large and small stimuli moving at 1°/s.

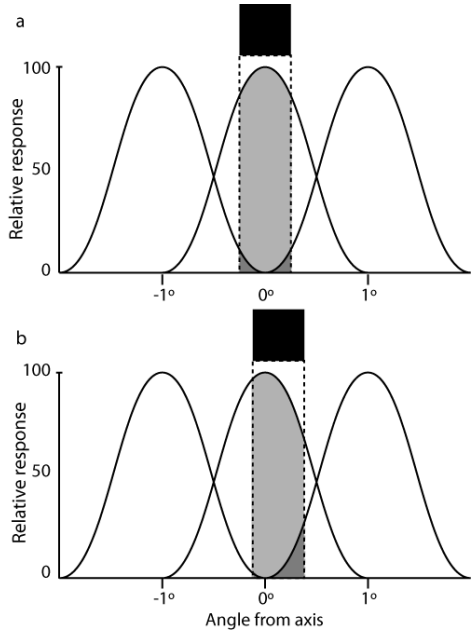


Figure.4. Hypothetical angular sensitivity distributions of AL retina photoreceptors. Grey area under curves represents response of the photoreceptors to a square stimulus subtending 0.5°.a) Photoreceptor response to a centered stimulus b) stimulus displacement of 0.139° would lead to ca. 8.3% total change in response over 3 receptors.